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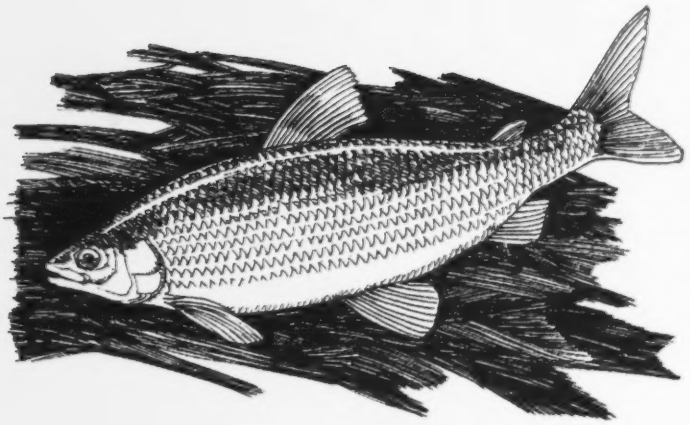
Status of the Shortjaw Cisco (*Coregonus zenithicus*) in Alberta

Mark Steinhilber



Alberta Wildlife Status Report No. 41

Alberta Conservation Association

Funded by Alberta Anglers, Hunters and Other Conservationists

Alberta
SUSTAINABLE RESOURCE DEVELOPMENT

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PREFACE

Every five years, the Fish and Wildlife Division of Alberta Sustainable Resource Development reviews the status of wildlife species in Alberta. These overviews, which have been conducted in 1991, 1996 and 2000, assign individual species "ranks" that reflect the perceived level of risk to populations that occur in the province. Such designations are determined from extensive consultations with professional and amateur biologists, and from a variety of readily available sources of population data. A primary objective of these reviews is to identify species that may be considered for more detailed status determinations.

The Alberta Wildlife Status Report Series is an extension of the general statusing exercises (1996 *Status of Alberta Wildlife, The General Status of Alberta Wild Species* 2000), and provides comprehensive current summaries of the biological status of selected wildlife species in Alberta. Priority is given to species that are potentially at risk in the province ("At Risk," "May Be At Risk"), that are of uncertain status ("Undetermined"), or those considered to be at risk at a national level by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

Reports in this series are published and distributed by the Alberta Conservation Association and the Fish and Wildlife Division of Alberta Sustainable Resource Development. They are intended to provide detailed and up-to-date information which will be useful to resource professionals for managing populations of species and their habitats in the province. The reports are also designed to provide current information which will assist the Alberta Endangered Species Conservation Committee to identify species that may be formally designated as "Endangered" or "Threatened" under Alberta's *Wildlife Act*. To achieve these goals, the reports have been authored and/or reviewed by individuals with unique local expertise in the biology and management of each species.

EXECUTIVE SUMMARY

The shortjaw cisco is currently designated "Threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as a result of overexploitation and habitat degradation in the Great Lakes. It is currently ranked "May Be At Risk" in Alberta. This ranking is based on status definitions outlined in *The General Status of Alberta Wild Species 2000* (Alberta Sustainable Resource Development 2001). This report reviews and summarizes recent and historical information on the shortjaw cisco as a step in further assessing its status in Alberta.

The only verified report of shortjaw cisco in Alberta is from Barrow Lake in the Canadian Shield region of the province. Reports from two other sites, Lake Athabasca and Gregoire Lake southeast of Fort McMurray, are questionable. The taxonomy, ecology, and distribution of shortjaw cisco in northeastern Alberta are currently being re-examined. Results to date suggest the Barrow Lake population resembles known shortjaw cisco morphologically and genetically. Ecologically, this population differs from "typical" shortjaw cisco populations in that it occupies shallow water habitats. Feeding and reproduction appear to be similar to populations at other localities. Preliminary catch-per-unit-effort data suggest the population in Barrow Lake is stable, although more data are required to estimate absolute population size and to assess sampling variance and the predictive power of abundance trends. Surveys of 18 lakes in the area around Barrow Lake from 1996 to 2001 failed to locate any additional populations of this species. Samples from Cold Lake–the site of an unverified historical report of shortjaw cisco–were also analyzed and determined to represent lake herring. Voucher specimens of cisco from all fisheries inventory projects in northern Alberta should be examined carefully and deposited in a museum for future analysis.

The factors that have caused the decline in shortjaw cisco populations in the Great Lakes (commercial overfishing, habitat degradation, competition with introduced species, and sea lamprey predation) are currently of little consequence to Alberta shortjaw cisco. Natural factors such as competition and introgression with sympatric lake herring may pose the greatest risk to the persistence of this species in the province. Anthropogenic factors that may upset the delicate ecological balance in Barrow Lake, and any other lakes in which shortjaw cisco may eventually be found, should be considered carefully in future management strategies.

ACKNOWLEDGEMENTS

Thanks to Thomas Todd of the Great Lakes Science Center for providing information on shortjaw cisco in the Great Lakes area and for supplying a draft of his COSEWIC report currently in preparation. Wayne Roberts (University of Alberta Museum of Zoology) and Erling Holm (Royal Ontario Museum) facilitated access to specimens housed in these institutions. Darlene Balkwill and Sylvie Laframboise (Canadian Museum of Nature) and Dr. William Preston (Manitoba Museum of Man and Nature) kindly supplied data on shortjaw cisco holdings in their collections. Larry Rhude (Alberta Sustainable Resource Development, Fisheries Management) provided information dealing with the management of shortjaw cisco in Alberta. Wes English (Alberta Sustainable Resource Development, Fisheries Management) provided cisco specimens from Cold Lake. Acquisition of much of the northeastern Alberta data presented herein would not have been possible without the field assistance of Stephen Petersen, Matthew Thompson, Guy Hawkings, Nathan Erik, Dominique Simard, Bryan Adcock, and Brian Meagher. A special thank you to Dr. Joseph Nelson (University of Alberta, Department of Biological Sciences) for supervising the initial study of the systematics of shortjaw cisco in Barrow Lake. Funding for that research was provided in part by the Challenge Grants in Biodiversity program, Alberta Conservation Association and by the Northern Scientific Training Program, Canadian Circumpolar Institute. Thanks to Jim Burns (Provincial Museum of Alberta), Joseph Nelson (University of Alberta), Mike Sullivan (Alberta Sustainable Resource Development), James Reist (Fisheries and Oceans Canada), Thomas Todd (Great Lakes Science Center, United States Geological Survey), Robin Gutsell (Alberta Sustainable Resource Development), and Sherry Feser (Alberta Conservation Association) for reviewing this manuscript.

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INTRODUCTION

Ciscoes, along with whitefishes and inconnu, are members of the subfamily Coregoninae. Nelson (1994) places these in the family Salmonidae along with the graylings and the trout and the salmon. Ciscoes are freshwater and anadromous fishes (live much of their life in the ocean but spawn in fresh water) with typical trout-like bodies (terete shape, abdominal pelvic fins, adipose fin present) but with larger scales than trout or salmon and no teeth on the bones of the jaws. They are Holarctic in distribution with many species endemic to North America or Eurasia.

The shortjaw cisco (*Coregonus zenithicus*) occurs only in northern North America, from the Great Lakes and southeastern Ontario to Great Slave Lake, Northwest Territories. It was once common in most of the Great Lakes but its numbers have declined dramatically since about the middle of the last century. It is now listed as "Threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002). In 1969, the shortjaw cisco was reported from Barrow Lake in northeastern Alberta (Paterson 1969). They were found to co-occur there with the widespread and abundant cisco or lake herring[1], *C. artedi* LeSueur 1818. To date, this remains the only verifiable report of a cisco other than lake herring in the province. Records of this species from Gregoire Lake near Fort McMurray (Tripp and Tsui 1980) and from the Alberta side of Lake Athabasca (Dymond and Pritchard 1930) are noted in Nelson and Paetz (1992) but remain questionable and unverified. The shortjaw cisco has a very limited distribution in Alberta, and according to *The General Status of Alberta Wild Species 2000* it is currently ranked "May Be At Risk"[2] in the province (Alberta Sustainable Resource Development 2001). This report is intended to compile and summarize historical and recent information on the status of the shortjaw cisco in Alberta.

HABITAT

The shortjaw cisco is primarily a lake dweller, although it is occasionally encountered in flowing waters. It is considered a deep-water species, preferring cold, well-oxygenated water below the thermocline (see glossary, Appendix 2). In the Great Lakes, the shortjaw cisco is usually found at depths ranging from 18-183 m (Van Oosten 1937), although it was widely distributed vertically and horizontally in Lake Superior and was always found over abruptly sloping substrates at depths of about 55 – 145 m (Koelz 1929). In George Lake, Manitoba, and Sandy Lake, Ontario, the shortjaw cisco also inhabits only the deepest regions of the lake (T. Todd pers. comm.). In Lake Athabasca, specimens believed to be shortjaw cisco were found primarily in water deeper than 20 m in the Black Bay area near Uranium City, Saskatchewan (Steinhilber 2002). Turgeon et al. (1999), however, found ciscoes resembling the shortjaw cisco to be common in shallow and midwater layers of Lake Nipigon. Bajkov (1930) reported that the shortjaw cisco in lakes Winnipeg, Winnipegosis, and others also prefer shallow water (4-10 m). Paterson (1969) found the shortjaw cisco only in very shallow water (2-5 m depth) in Barrow Lake, Alberta and Steinhilber (2000 and unpublished data) captured this species at depths of 5-16 m in Barrow Lake (Figure 1). These latter data do not simply reflect an inhospitable (anoxic) environment at greater depths in Barrow Lake, since many co-occurring lake herring were collected from the deepest areas of the lake (24 m) during the same time period (Figure 1). Therefore, it appears that the species currently recognized as the shortjaw cisco is adaptable and tolerant of a wide range of habitats.

---

[1] This is the only North American fish with two formally accepted common names (Robins et al. 1991). While "cisco" tends to be the preferred name in western North America, "lake herring" has been used in this document to avoid confusion and awkwardness when discussing "ciscoes" as a group (more than one species – "es" ending) and "cisco" when referring to many individuals of one species, or to *C. artedi*.

[2] See Appendix 1 for definitions of selected status designations.

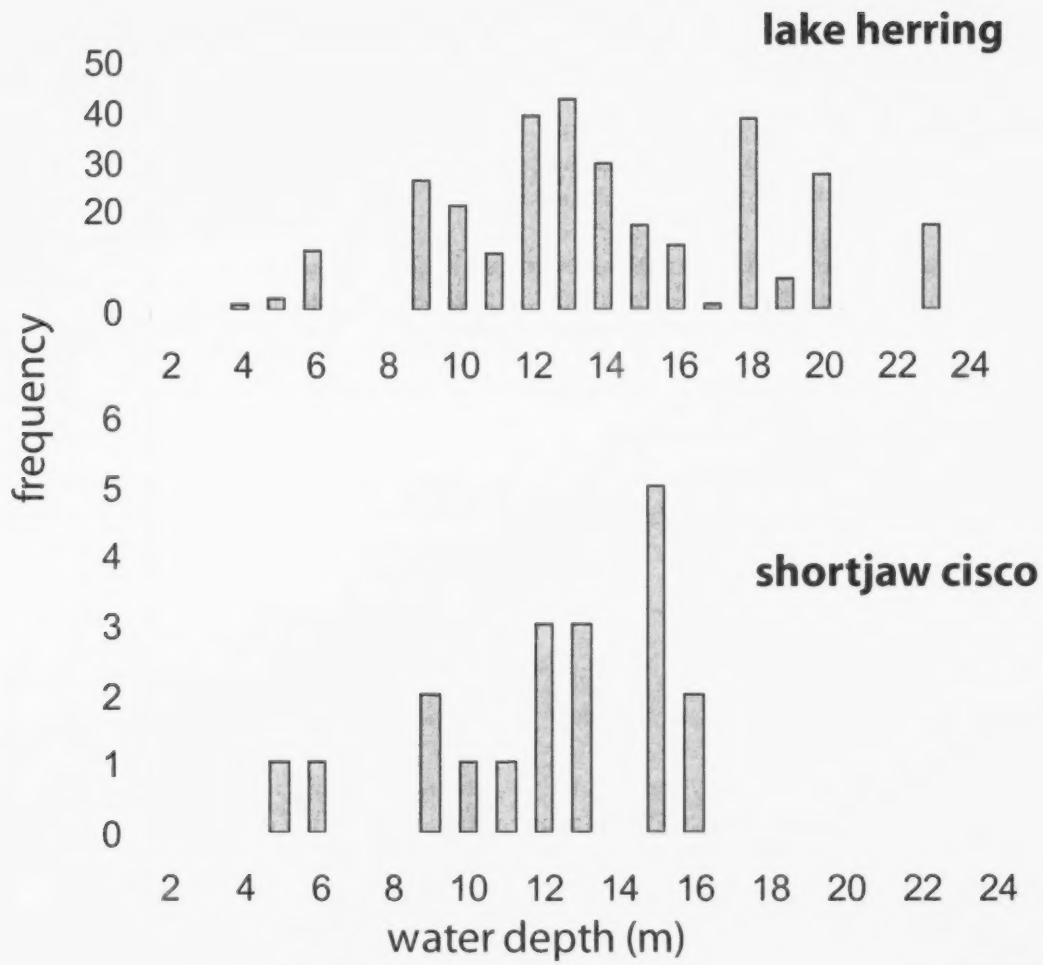

Figure 1. Water depth at point of capture of shortjaw cisco and lake herring in Barrow Lake. No shortjaw cisco were encountered in water deeper than 16 m.

Ciscoes as a group are characterized as residents of the pelagic zone (see glossary, Appendix 2) of lakes. However, the shortjaw cisco appears to be more closely associated with the lake bottom than are lake herring. Although the shortjaw cisco diet occasionally consists of a portion of limnetic (see glossary, Appendix 2) crustaceans like copepods and cladocerans (e.g., *Daphnia* spp.) (Koelz 1929, Scott and Crossman 1973), epibenthic (see glossary, Appendix 2) prey like opossum shrimp (*Mysis relicta*), the deepwater amphipod *Pontoporeia*, and larvae of aquatic insects (e.g., chironomids) make up the majority of the diet of this species (Bajkov 1930, Scott and Crossman 1973). In Barrow Lake, the shortjaw cisco consumed *Mysis relicta* almost exclusively during the open water season (Figure 2). Insignificant numbers of copepods and cladocerans combined with occasional pelecypods (clams) and bits of detrital (see glossary, Appendix 2) material suggest this species feeds near, but not on, the bottom (Steinhilber 2000).

Gillnetting data provide evidence that the shortjaw cisco in Barrow Lake are most active during daylight hours (M. Steinhilber, unpublished data). Most specimens were captured between 9 a.m. and 9 p.m. with relatively few encountered in overnight sets.

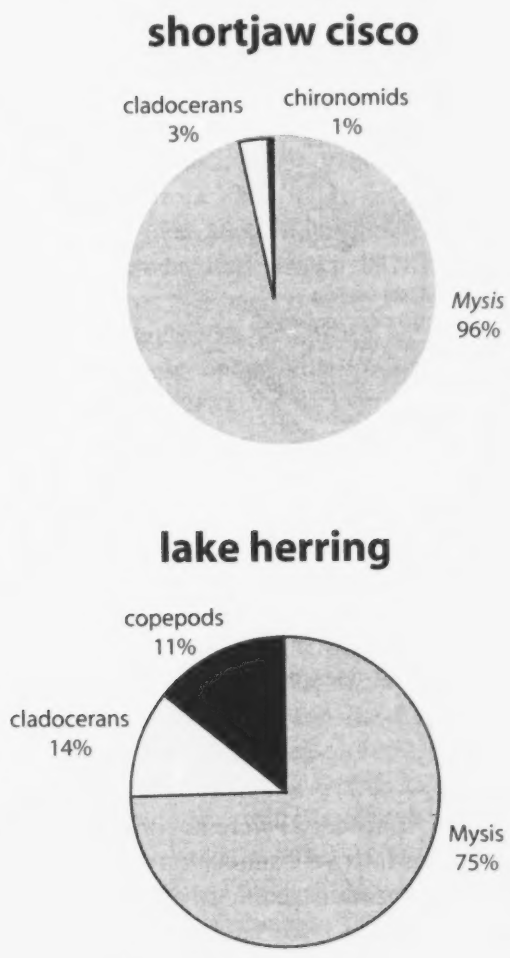

Figure 2. Diet of shortjaw cisco and lake herring in Barrow Lake. Although lake herring consumed more plankton (copepods and cladocerans) than shortjaw cisco, both species fed primarily on oppossum shrimp (*Mysis relicta*).

During the day, *Mysis relicta* is also found near the bottom, moving upward in the water column as light levels decrease (Clifford 1991, Gal et al. 1999). Therefore, it seems likely that the Barrow Lake shortjaw cisco is primarily a diurnal or crepuscular feeder consuming *Mysis relicta* while these prey are concentrated near the bottom of the lake.

CONSERVATION BIOLOGY

1. Identification. - Members of the genus *Coregonus* are notoriously variable morphologically. There are persistent taxonomic questions that have made accurate identifications of some species of this genus difficult. Not only are all cisco species similar in overall appearance, but parallel evolution, hybridization, local adaptation, and phenotypic plasticity are believed to have interacted in varying degrees to produce a confounding array of forms and species that often defy traditional classification. Resolving the taxonomic question of what a shortjaw cisco is, must be the first step in the management of this species. The key morphological and genetic characters that unequivocally define the shortjaw cisco have been elusive.

The number of gillrakers (see glossary, Appendix 2) appears to be one of the best characters for separating some cisco species. The known range of the shortjaw cisco gillraker number is 30 - 46 (Scott and Crossman 1973, Steinhilber 2000). However, 98% of specimens examined from sites throughout North America (n=122) had 44 gillrakers or fewer (M. Steinhilber, unpublished data). This is usually less than gillraker counts for the lake herring – the species most likely confused with the shortjaw cisco outside of the Great Lakes. Lake herring gillraker counts can range from 38 to 64 (Scott and Crossman 1973); however, 98% of Alberta specimens examined (n=665) had 42-59 gillrakers (M. Steinhilber, unpublished data).

In combination with a low gillraker count, the shortjaw cisco usually can be distinguished from the lake herring by its longer snout, shorter gillrakers, longer upper jaw, its lower jaw that does not extend beyond the upper jaw, and its more vertical premaxillaries (Todd and Smith 1980). In addition, the Barrow Lake population in Alberta can be separated from the co-occurring lake herring by a larger size, shallower head, smaller eye, and longer dorsal fin (Steinhilber

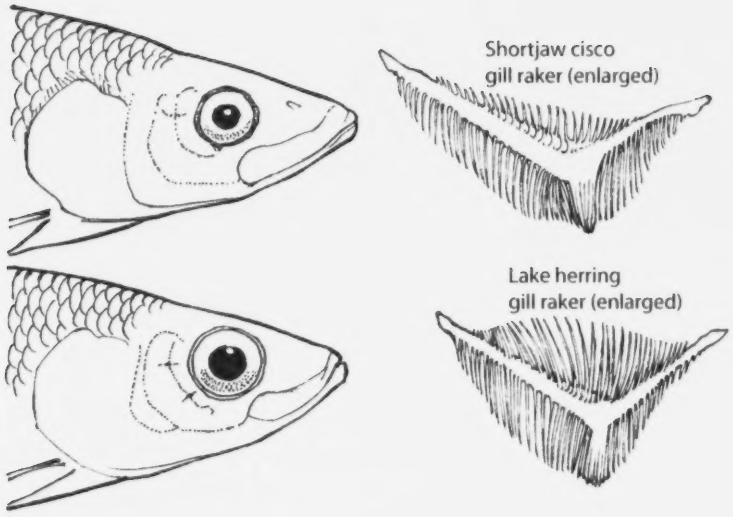

Figure 3. Shortjaw cisco (above) and lake herring (below) from Barrow Lake. Shortjaw cisco have fewer and shorter gillrakers, a longer upper jaw, longer snout with a more vertical tip, smaller eye, shallower head, and a lower jaw that does not protrude beyond the upper jaw.

2000) (Figure 3). Local variation can obscure some of these traits in some populations; thus, caution must be exercised when attempting to identify ciscoes based on one or a few characters. All Alberta cisco populations with mean gillraker counts less than 44 should be examined carefully and voucher specimens should be retained for future analysis and verification of identity.

2. Reproduction. - Like most members of the whitefish subfamily, the shortjaw cisco usually spawns in the fall, although spring spawning has been reported in Lake Superior (Todd and Smith 1980). It is believed that these spring spawners are not simply occasional out-of-season spawners but may represent a distinct population. The exact time of fall spawning varies from lake to lake, but usually occurs from late September to early December (Koelz 1929, Scott and Crossman 1973). In Barrow Lake, specimens collected in the first two weeks of October 1997 had not yet spawned and did not extrude eggs or milt when gentle pressure was applied to the abdomen (pers. obs.). Nuptial tubercles (see glossary, Appendix 2) were not present on any specimens. Internal examination revealed well-developed gonads suggesting that this population probably spawns in the fall but not until at least late October or November. However, mature gonads do not necessarily mean spawning is imminent; in some fishes, gonads reach advanced stages of development in the fall even though spawning does not occur until the following spring (M. Sullivan, pers. comm.). The co-occurring lake herring exhibited a similar level of gonad maturation and tubercle development thus providing no conclusive evidence for reproductive isolation between species via spawning allochrony (see glossary, Appendix 2).

The shortjaw cisco is a broadcast spawner, depositing its eggs over various substrates (often clay bottoms in the Great Lakes) without building a nest or providing any parental care. Eggs develop over the winter and hatching occurs in the spring. The rate of development is determined primarily by water temperature.

Little is known about the fecundity of the shortjaw cisco although it has been suggested that egg production is likely similar to that of a closely related deepwater cisco, the bloater (*C. hoyi*) (T. Todd, pers. comm.). The bloater produces from 3000 (for an individual 241 mm long) to over 18 000 eggs for a fish 305 mm long (Emery and Brown 1978). Spawning behaviour has been described as completely promiscuous with no fighting, nipping, chasing, threatening, or other aggressive behaviour (Svärdson 1965).

Spawning sites in Barrow Lake are unknown, although Turner (1967) believed that little suitable spawning habitat was available. Limited spawning sites and indiscriminant broadcast spawning behaviour of both the shortjaw cisco and the lake herring increase the probability of hybridization between these species. Most species of cisco have been shown experimentally to be inter-fertile (Svärdson 1957, 1970, Garside and Christie 1962); however, no apparent hybrids were found in a sample of 360 ciscoes from Barrow Lake (Steinhilber 2000). It is possible that selection of different spawning sites could be partially responsible for the reproductive isolation between the shortjaw cisco and the lake herring. Any habitat degradation that causes a reduction in the number of the already limited spawning sites could contribute to the breakdown of this isolating mechanism and lead to introgression (see glossary, Appendix 2) of the two gene pools.

The age at which the shortjaw cisco becomes reproductively mature varies among sites. In Lake Winnipeg, spawning began at age four (about 250 mm long) and mature individuals spawned every year after that (Bajkov 1930). Lake Superior specimens examined by Van Oosten (1937) usually showed maturing sex organs 150 mm in length and almost all were mature by 200 mm standard length[3]. In Barrow Lake, two-year-old females that were about 250 mm standard length were found to contain ova of the same diameter as individuals five years or older (unpublished data). Based on the gonad maturation scale of Nikolsky (1978), this suggests that the female shortjaw cisco in Barrow Lake begin spawning at age two. The data are less conclusive for males, although it appears that development of the testes increases dramatically between age two and three (about 220 mm to 270 mm standard length) suggesting most males may not spawn until their third year.

Although there is little sexual dimorphism in the shortjaw cisco, females, on average, may be slightly larger and heavier than males of corresponding age-groups. However, there do not appear to be significant differences in growth rate between sexes or age-classes after the first year (Van Oosten 1937). Clarke (1973) found little evidence for sexual dimorphism in a large sample of many cisco populations across North America. Similarly, Steinhilber (2000) found that few characters showed statistically significant sexual dimorphism in the Barrow Lake shortjaw cisco or in six nearby populations of the lake herring.

3. Growth. - The shortjaw cisco displays a growth curve typical of many fish species. Increase in length is most rapid prior to maturation when energy is devoted primarily to growth of somatic tissues. Following maturation, much energy is diverted from body growth to growth of gonadal tissues (Moyle and Cech 1988). Van Oosten (1937) found the growth increment in first-year shortjaw cisco of Lake Superior to be three times that of any of the subsequent five years. Following maturity, the rate of growth in length declined but remained relatively constant from years two through six. Another rate decrease at age seven was followed by a period of uniform growth until about age nine. Unlike length, the greatest increase in weight occurred around the fifth year.

[3] Standard length (SL) is measured from the tip of the snout to the end of the bony support for the tail. This point can usually be found by flexing the tail fin rays so that a crease forms where the rays meet the bony support (hypural bones).

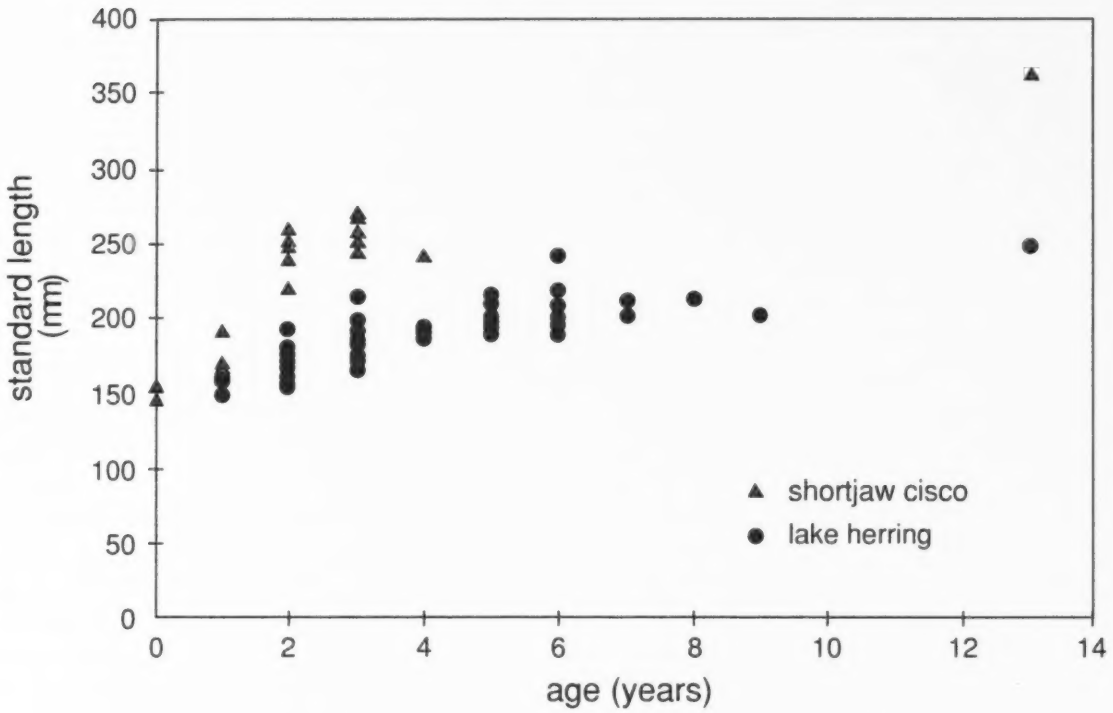

Figure 4. Length-at-age relationship for Barrow Lake shortjaw cisco and lake herring. Shortjaw cisco appear to grow faster than sympatric lake herring in the first few years of life and attain a larger adult size. The two age 0+ shortjaw cisco specimens, approximately 150 mm in length, were collected in October of 1997 and had probably completed their first year of growth. These are exceptionally large young-of-the-year when compared with specimens of the same age from Lake Superior (calculated lengths - Van Oosten 1937) and Lake Winnipeg (Keleher 1952). This may be due to the larger size of adult Barrow Lake specimens relative to the Lake Superior and Lake Winnipeg populations, although it should be noted that ages were not validated.

The length-at-age relationship for the Barrow Lake cisco is shown in Figure 4. It appears that the shortjaw cisco in this lake grow more rapidly than the sympatric lake herring, especially in the first three or four years of life (Steinhilber 2000). These data also provide conclusive evidence that the smaller lake herring do not simply represent young age classes, nor do the larger shortjaw cisco represent older age classes of the same population – a possibility raised by Paterson (1969). Individuals of both species as old as 13 years were found (Figure 4). Although only one shortjaw cisco specimen larger than 400 mm fork length was acquired in this study, several specimens collected by Paterson (1969) were also in this size range (see Appendix 2). Rapid attainment of a relatively large size undoubtedly confers some advantages to the shortjaw cisco with respect to predation by northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), and burbot (*Lota lota*) (see limiting factors section). Individual ciscoes approximately 150 mm in length appear to represent the preferred prey size for these predators (M. Steinilber pers. obs.). Attacks on gillnetted specimens of this size were common. However, rarely did individuals over 200 mm in length show evidence of attempted predation. It is interesting to note that the Barrow Lake shortjaw cisco grows to the largest size of any known population of this species in North America (Koelz 1929, Clarke 1973, Steinhilber 2000).

DISTRIBUTION

1. Alberta. - In Alberta, the only verified population of the shortjaw cisco is in Barrow Lake in the Canadian Shield region of the northeastern corner of the province (Figure 5). Reports of this species from the Alberta side of Lake Athabasca (Dymond and Pritchard 1930), from Gregoire Lake near Fort McMurray (Tripp and Tsui 1980), and from Cold Lake (Clarke 1973) are questionable and require confirmation (Nelson and Paetz 1992). A recent survey in the southern portion of Lake Athabasca, west of the Alberta-Saskatchewan border, failed to confirm the presence of the shortjaw cisco in this area (Steinhilber 2002.). However, approximately one-third of the ciscoes collected in Black Bay on the Saskatchewan side of Lake Athabasca had low gillraker counts and are believed to be shortjaw cisco (Steinhilber 2002). This would represent the nearest known population of this species to Barrow Lake. The extant connection between these populations (through southeastern Lake Athabasca to Riviere des Rochers, the Slave River, and Ryan Creek) includes large areas of habitat that appear unsuitable for shortjaw cisco (Steinhilber 2000). The probability that these populations have intermixed post-glacially is remote. While they share the key identifying character of few gillrakers, the forms in Barrow Lake and Lake Athabasca are distinctly different in body size. The Barrow Lake form is the largest known shortjaw cisco in North America (Steinhilber 2000); the Lake Athabasca form is relatively small. This suggests that isolation and local adaptation have contributed to morphological divergence of these populations. Analysis of 100 cisco samples collected as part of a lake trout survey at Cold Lake in 2001 did not confirm the existence of shortjaw cisco at this site. However, a single low gillraker individual exhibited unique morphological features that suggest it may be a shortjaw cisco (Steinhilber 2002). This individual had 39 gillrakers (all other specimens had 42-53), an extraordinarily short dorsal fin base (a characteristic of many shortjaw cisco populations throughout North America), and an ovary in an advanced state of development (suggesting it may spawn earlier than the other specimen in the sample).

Additional sampling at Cold Lake, and an analysis of independant character sets from the ciscoes acquired, is needed to verify if a popuation of shortjaw cisco occurs at this site. Surveys conducted in 1996, 1997, 2000, and 2001 (Steinhilber 2000, and unpublished data) in 17 lakes in the Canadian Shield region near Barrow Lake found no additional populations of the shortjaw cisco (Figure 6). Two sympatric cisco populations in Winnifred Lake, a "dwarf" and a "normal" form, both exhibited gillraker counts from 39 – 46 (n=11, dwarf form; n=18, normal form). This falls within the known range of gillraker number for the shortjaw cisco across North America, although it also overlaps extensively with the low end of counts from the lake herring across the range of that species. Preliminary analyses based on other key morphological characters (e.g., upper jaw length, head depth) suggest that these forms are not the shortjaw cisco but rather low gillraker variants of the lake herring. Further morphological and genetic analyses are underway to confirm this identification. At present, Barrow Lake remains the only confirmed locality for the shortjaw cisco in Alberta. The surface area of the lake is 3.81 km^2 (Turner 1967). This value can be used as an estimate of the area of occupancy for this species in Alberta. The proportion of the range of this species that occurs in Alberta is, therefore, < 1% although that may increase slightly if new populations are discovered or unconfirmed reports are verified.

2. Other Areas. - The shortjaw cisco has a wide but sporadic distribution in northern North America (Figure 6). It was formerly present in all of the Great Lakes, with the possible exception of Lake Ontario, where Koelz (1929) did not record it in an exhaustive study. Todd and Smith (1992) believe that the shortjaw cisco has been extirpated in lakes Erie, Huron, and

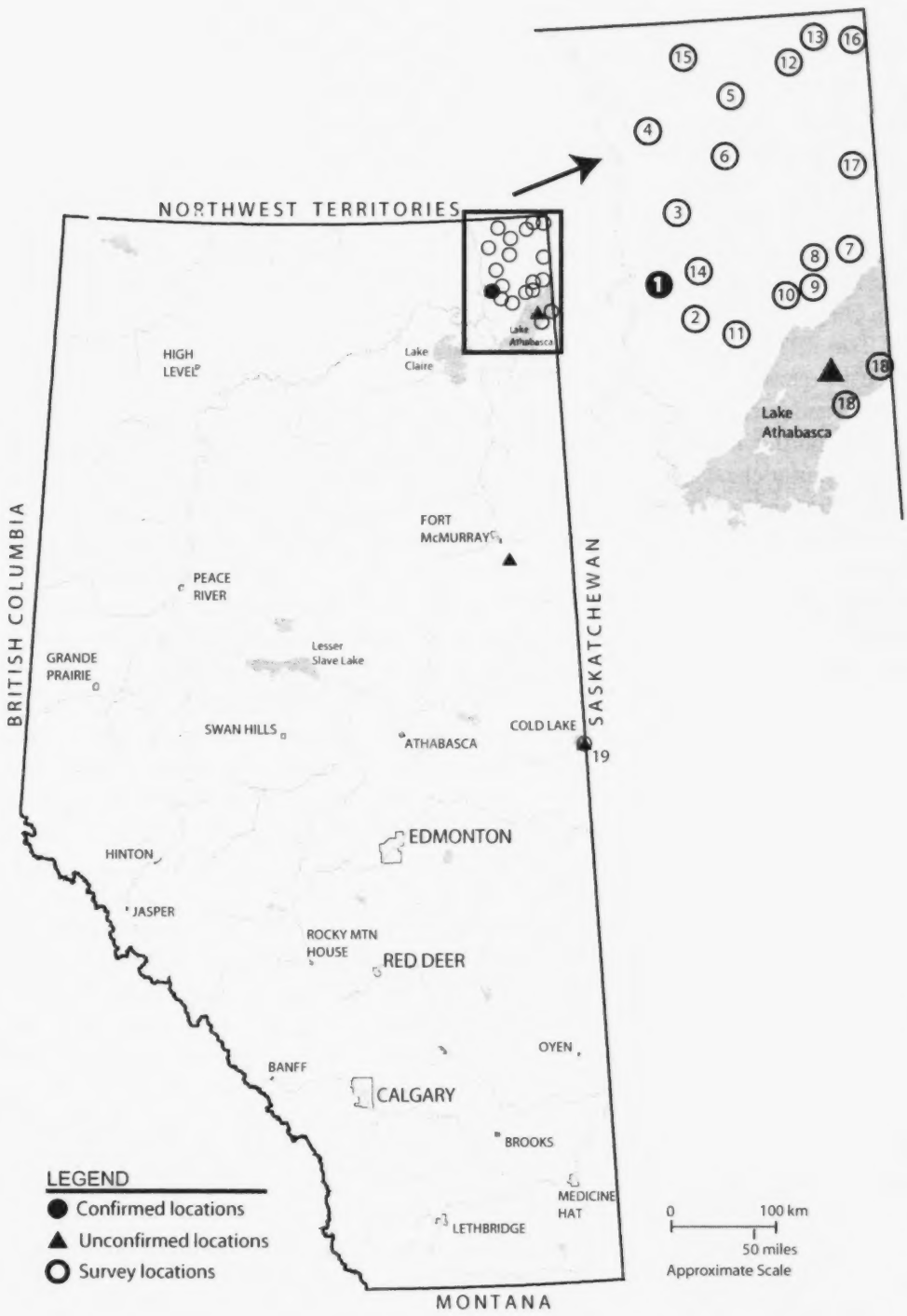

Figure 5. Known and unconfirmed localities for shortjaw cisco in Alberta. Open circles correspond to lakes sampled in 1996, 1997, 2000, and 2001 in search of shortjaw cisco: 1) Barrow Lake, 2) Ryan Lake, 3) Bocquene Lake, 4) Myers Lake, 5) Unnamed Lake #1, 6) Daly Lake, 7) Burstall Lake, 8) Wylie Lake, 9) Winnifred Lake, 10) Unnamed Lake #2, 11) Fletcher Lake, 12) Dawson Lake, 13) Bayonet Lake, 14) Darwin Lake, 15) Leland Lake, 16) Andrew Lake, 17) Colin Lake, 18) Lake Athabasca, 19) Cold Lake.

Figure 6. The distribution of shortjaw cisco across North America. See Appendix 3 for details of each site record for extant populations.

Michigan (along with Lake Ontario, if it was ever present there) and is rare in Lake Superior. Only Lake Nipigon continues to support a good population of this species (Todd and Smith 1992, Turgeon et al. 1999).

Outside of the Great Lakes basin, the shortjaw cisco has been found sporadically throughout northern Canada from southeastern Ontario to Great Slave Lake, Northwest Territories (Clarke 1973, Scott and Crossman 1973). However, the full range of this species remains poorly known. Localities from which museum specimens have been acquired and preserved, as well as sites in the literature suggested to contain shortjaw cisco, are shown in Figure 6. Appendix 3 lists details of these reports. The extent of occurrence (IUCN 2001) of the shortjaw cisco covers approximately 1.5 million km^2. However, the area of occupancy within this range is estimated herein at about 100 000 km^2 (7% of the extent of occurrence). This figure is based on the combined area of the six largest lakes known to contain shortjaw cisco (lakes Superior, Nipigon, Winnipeg, Reindeer, Athabasca, and Great Slave) (Natural Resources Canada 2000) and assumes that the smaller lakes account for <1% of the area of occupancy. This low value indicates a widely scattered population distribution that may, in part, reflect inadequate sampling effort or the taxonomic uncertainties surrounding ciscoes at these sites.

Important questions regarding the taxonomy of North American ciscoes, and particularly the validity of the shortjaw cisco as a distinct species, remain unanswered. Recent genetic analyses show a striking similarity between the DNA of the shortjaw cisco and the lake herring (Reed et al. 1998, Turgeon et al. 1999, Steinhilber et al. 2001). This suggests that what we currently consider to be the shortjaw cisco may represent a consistently recurring low gillraker form of the lake herring. It should be cautioned that these genetic data are still inconclusive. The major evolutionary radiation of North American ciscoes probably occurred as recently as 100 000-250 000 years ago (Bailey and Smith 1981, Smith and Todd 1984, Reed et al. 1998), and major genetic differences among species would not be expected after such a short time period.

Parallel evolution among isolated populations of the lake herring, especially outside of the Great Lakes, may be producing morphologically equivalent forms that resemble the shortjaw cisco despite no genetic linkage among populations or to a common shortjaw cisco ancestor. To further complicate matters, it is possible that more than one true form of the shortjaw cisco exists in northern Canadian lakes (Todd and Steinhilber 2001) and that these are interspersed with forms of the lake herring (and possibly other species) that superficially resemble the shortjaw cisco. Although parallel evolution is a possibility, the argument for this mechanism is weakened by the morphological similarities exhibited by the shortjaw cisco from widely different habitats across North America. The evolution of structural similarities among unrelated organisms is usually driven by exposure to similar environmental pressures to which the organisms adapt in similar ways. The shortjaw cisco lives in a range of habitats from deep water in the Great Lakes to shallow regions of small water bodies like Barrow Lake; yet these populations continue to share many key morphological characteristics. Multivariate analyses have shown that populations of the shortjaw cisco form a cluster on ordination plots distinct from the lake herring (Steinhilber 2000). These data suggest the shortjaw cisco is a valid species and should be managed accordingly until evidence indicates otherwise. Further work is underway to resolve this issue, and highlights the critical need to obtain and preserve voucher specimens for current and future research into this complex problem.

There is little evidence available on the historic distribution of the shortjaw cisco outside of the Great Lakes basin. Most of the non-Great Lakes range of this species includes areas relatively undisturbed by human activity. Anthropogenic factors have likely had little influence on the

distribution or abundance of this species in northern Canada. It is interesting to note that, with the exception of the George Lake, Manitoba population, most populations of the shortjaw cisco occur sympatrically with one or more other species of cisco – most commonly the lake herring. Competitive interactions between co-occurring species may constitute the greatest threat to the continued existence of shortjaw cisco in these situations. Competitive exclusion and/or introgression have likely contributed to the current population size and distribution patterns of the species. Further work, on a population-by-population basis, is required to determine the degree of ecological and reproductive isolation among co-occurring populations of these ciscoes.

POPULATION SIZE AND TRENDS

1. Alberta. - Little is known about the shortjaw cisco population trends in lakes outside the Great Lakes basin. In Barrow Lake, relative abundance and catch-per-unit-effort (CPUE) data collected by Paterson (1969) and Steinhilber (2000, unpublished data) tentatively suggest that the population has been stable over the past three decades. Twenty-three shortjaw cisco specimens were collected at Barrow Lake between 2 and 5 August, 2000. This represented 11.6% of the 199 ciscoes collected in total (the remainder were lake herring). The catch of the shortjaw cisco was calculated to be 0.00078 specimens/hour/m^2 of net. This compares with 0.00031 specimens/hour/m^2 of net in July 1996 (n=153; 4.6% of the total catch of ciscoes), 0.00035 specimens/hour/m^2 of net in July 1997 (n=158; 5.7% of the catch), and 0.00013 specimens/hour/m^2 of net in October 1997 (n=72; 4.2% of the catch). CPUE from these surveys was compared with gillnetting data published by Paterson in 1969 and unpublished data prepared by Turner in 1967 (both datasets are based on the same survey). To enhance comparability, only specimens collected in Paterson and Turner's 3.8 cm, 6.4 cm, and 8.9 cm stretched mesh nets were used. (They also set larger mesh sizes that were not used in the current study. It was assumed that all ciscoes captured in their 10.2 cm, 11.4 cm, and 14.0 cm mesh nets were shortjaw cisco because of the much larger size of this species compared with the sympatric lake herring.). Catch of the shortjaw cisco per unit effort for these mesh sizes was estimated at 0.000433 specimens/hour/m^2 of net – a value comparable to that found in the current study. Therefore, based on this limited data, it appears that the population of the shortjaw cisco in Barrow Lake has been relatively stable over at least the past five years and possibly the last 30 years. However, it must be cautioned that distinguishing short-term population fluctuations from long-term trends requires many more data points than are available at this time. The current data are insufficient to calculate a meaningful percent change over time or an estimate of total abundance. Continued monitoring using standardized protocols is needed to assess sampling variance and the predictive power of these data.

2. Other Areas. - From the mid-19th century until the mid- to latter part of the 20th century, the shortjaw cisco was a prominent component of the fish fauna of most of the Laurentian Great Lakes (Koelz 1929, Fleischer 1992). In the 1920s, about 17% of the Lake Huron "chub" fishery (a term referring to most deepwater cisco species combined) consisted of the shortjaw cisco (Koelz 1929), and in 1956 this species made up about 19% of the chub catch (Todd 2001). In the late 1930s, the shortjaw cisco was the only large chub in Lake Superior common enough to be commercially viable (Van Oosten 1937). By about the middle of this century, however, the cisco populations in the Great Lakes began to decline. In Lake Michigan, species of intermediate size (including the shortjaw cisco) comprised 66% of the deepwater cisco stocks in the 1930s, 23.9% in the 1950s, and 6.4% in the 1960s (Smith 1964). By the early 1970s, the shortjaw cisco was considered extirpated from this lake (Todd and Smith 1992). In Lake Huron, the shortjaw cisco was extremely

rare by the 1970s and were extirpated by 1982 (T. Todd, pers. comm.). No population trend data are available for Lake Erie (T. Todd, pers. comm.), but as of 1992 it was considered extirpated from this lake as well (Todd and Smith 1992). The shortjaw cisco still occurs in Lake Superior, but has decreased in abundance from 90% of the chub catch in the 1920s (Koelz 1929) to 6-11 % in the 1970s (Peck 1977) and 5–11% in 1997 (Todd 2001). Only in Lake Nipigon is it still considered abundant (Todd and Smith 1992). A study on the abundance and distribution of shortjaw cisco in Lake Superior is currently being conducted by Mike Hoff and Tom Todd of the Great Lakes Science Center (T. Todd, pers. comm.).

LIMITING FACTORS

In the Great Lakes, commercial overfishing, habitat degradation, competition with exotic species, particularly alewives (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax)*, and predation by sea lamprey (*Petromyzon marinus*) have caused severe reductions in coregonine populations and the extinction of several species (Smith 1964, Fleischer 1992). Fortunately, the fishery and environmental impediments to the recovery of ciscoes in the major Great Lakes have now been removed in large part. This should promote the re-establishment of some species into their former habitats, assuming that adverse interactions with exotic species can be adequately controlled (Edsall 1999). In Lake Nipigon, ecological perturbations have been minimal relative to the other Great Lakes (Turgeon et al. 1999) and the shortjaw cisco still thrives here (Houston 1988). A recent invasion by the rainbow smelt in 1976 is the only stressor that significantly affects this population (Salmon and van Ogtrop 1996).

Global warming is predicted to have a major impact on aquatic ecosystems worldwide (US EPA 1995). The most obvious effect of a warmer, drier climate is the potential for the desiccation of many water bodies and their associated biodiversity. However, other subtle and complex interactions are also predicted for boreal lakes based on temperature changes resulting from an approximate doubling of atmospheric CO_2 concentrations. An increase in solar energy input, combined with a decrease in dissolved organic carbon, is predicted to deepen the epilimnion (see Appendix 2, glossary of terms) in thermally stratified lakes smaller than about 500 hectares (Schindler et al. 1996, Fee et al. 1996, Talling and Lamoalle 1998). Increased wind velocity and wave action resulting from a combination of fire-induced forest denudation and a general increase in storm activity, may also contribute to a deepening of the mixed-water zone (Schindler et al. 1990). This will reduce the available habitat for species such as ciscoes that require the cool, well-oxygenated water of the hypolimnetic zone (see Appendix 2, glossary of terms) below the thermocline (see Appendix 2, glossary of terms) during the summer and could lead to extirpation of some species. A general warming of the epilimnion could have serious implications for important predatory species, particularly those that spend much of their lives in shallow, inshore (littoral) areas (e.g., the northern pike). Small increases in water temperature can stimulate manifold increases in the metabolic rates and food requirements of fishes. A study on immature lake trout (*Salvelinus namaycush*) found that a 3°C increase in mean July epilimnetic temperatures resulted in an 8- to 10-fold increase in the amount of food required to achieve a normal end-of-year body size (McDonald et al. 1996). This study concluded that juvenile growth could be enhanced under a climate change scenario if the necessary metabolic requirements can be met. However, if the food supply is limiting, as it often is, most individuals would starve to death before the end of their first year. The resulting decline in predator abundance would have disastrous implications for the ecology of many northern lakes.

None of the factors believed responsible for the declines of the shortjaw cisco in the Great Lakes appear to be an immediate threat to populations in northeastern Alberta. Human activity in the form of forestry, petroleum exploration, or mining is, as yet, minimal in the remote shield area of Alberta. Human-induced habitat degradation has not been a major factor in this region, although consideration should be given to any future activities that may disrupt the ecological balance in Barrow Lake and create potentially unfavourable conditions for the survival of the shortjaw cisco. Land-use activities that promote increased sediment or nutrient loading could lead to the eutrophication (see Appendix 2, glossary of terms) or the destruction of spawning areas. Improved access into this area may also encourage an increase in sport- or domestic fishing with direct and indirect effects on the shortjaw cisco population.

There are no records of any commercial fishing on Barrow Lake (L. Rhude, pers. comm. 2000). The extent of domestic fishing is unknown, but it is probably not significant given the remoteness of this lake. The large size of shortjaw cisco in Barrow Lake would make it particularly susceptible to capture in gill nets of mesh sizes suitable for capture of walleye, northern pike, and lake whitefish (*Coregonus clupeaformis*). In a small body of water like Barrow Lake, it is conceivable that moderate or even low levels of gillnetting pressure could reduce the shortjaw cisco population to nonviable levels, particularly if this stress is accompanied by unusually high natural mortality (e.g., summer- or winter-kills).

Some sportfishing, primarily for walleye and northern pike, does occur on Barrow Lake; however, records indicate that angling pressure on Barrow Lake has generally been low. A mean of 80 angler days was spent on Barrow Lake in each of five years on record with, on average, 30 walleye and 42 northern pike retained each year (L. Rhude, pers. comm. 2000). Although the current sportfishing pressure on Barrow Lake is minimal, overharvest of some species can occur with remarkably little angler effort (M. Sullivan, pers. comm. 2000). This is especially true in northern lakes where fish growth rates tend to be slow and maturation time prolonged. Although ciscoes are rarely taken by angling, gillnetting observations and stomach content analysis of walleye, pike, and burbot (unpublished data) indicate that the smaller lake herring are preferred by predatory species over the larger shortjaw cisco. Overfishing of these game species could cause the already abundant herring to increase in number, leading to increased competition with the shortjaw cisco. As the latter species becomes relatively rarer, the effect of introgression with the lake herring may increase (Svärdson 1965). These factors could pose a threat to the unique shortjaw cisco gene pool in Barrow lake.

STATUS DESIGNATIONS

1. Alberta. - According to *The General Status of Alberta Wild Species 2000*, the shortjaw cisco is currently ranked "May Be At Risk" in Alberta (Alberta Sustainable Resource Development 2001). The status of this species needs to be reviewed (Alberta Sustainable Resource Development 2001). The Alberta Natural Heritage Information Centre (ANHIC) ranks the shortjaw cisco as S1 based on few occurrences in the province (ANHIC 2001; see Appendix 1 for explanation of ranks).

2. Other. - The shortjaw cisco is designated "Threatened" by COSEWIC and has been since 1987 (Houston 1988, COSEWIC 2002). Population reduction resulting from exploitation and habitat loss is given as the reason for this designation. A recent COSEWIC evaluation (Todd 2001) reiterates the justification for alarm at the decline of this species in the Great Lakes. Globally, the shortjaw cisco is ranked G2 (NatureServe 2001) meaning the species is imperiled because of extreme rarity (see Appendix 1 for definitions of ranks). In Canada, NatureServe (2001) lists the subglobal (S) status

of this species as S1 in Saskatchewan, S2 in Ontario, S3 in Manitoba, and "uncertain" in the Northwest Territories and Nunavut. *Wild Species 2000: The General Status of Species* in Canada lists lists shortjaw cisco as "At Risk" in Ontario, "May Be At Risk" in the Northwest Territories, "Sensitive" in Manitoba, and "Undetermined" in Saskatchewan (CESCC 2001). In the northeastern United States, this species is ranked S1 in Indiana, S2 in Michigan, S3 in Minnesota, and S3? in Wisconsin (NatureServe 2001). Minnesota considers the shortjaw cisco a species of "Special Concern" (Minnesota Department of Natural Resources 2002) and in Michigan it is designated "Threatened" (Michigan Department of Natural Resources 1997). It is believed that the shortjaw cisco is extirpated from Illinois, New York, and Pennsylvania (NatureServe 2001).

RECENT MANAGEMENT IN ALBERTA

There is currently no management plan for the shortjaw cisco in Alberta (L. Rhude, pers. comm. 2000). No laws specifically protect this species, but general protection is afforded through federal and provincial *Fisheries Acts*. An ongoing study focusing on the taxonomy of this species in Barrow Lake has provided some life history and relative abundance data (Steinhilber 2000). Sixteen lakes in the Canadian Shield region near Barrow Lake have been surveyed by the author in a search for other Alberta populations of the shortjaw cisco. Ciscoes acquired as a result of research activities directed toward other fish species have been analyzed for two additional lakes (Leland and Cold lakes). Retention and analysis of cisco specimens encountered incidentally is a cost-effective means of providing additional distribution, abundance, and taxonomic data on these species. When appropriate, the collection of cisco voucher specimens should be considered in provincial fisheries studies.

SYNTHESIS

It is clear that the shortjaw cisco populations in the Laurentian Great Lakes have declined dramatically over the past 50 years and the likely causes of the decline are well documented. However, the anthropogenic factors likely responsible are probably of little consequence to populations of the shortjaw cisco outside the Great Lakes basin. The patchy distribution and low number of regional occurrences suggest this is likely a species that invaded northern North America postglacially via large proglacial lakes and was unable to tolerate conditions in many of the small remnants of those water bodies that remained following the disappearance of the ice and isostatic uplift (see glossary, Appendix 2). It is possible that the shortjaw cisco now persists in only a few localities, in some cases under suboptimal environmental conditions. The greatest threats to the survival of these unique populations are likely natural: competition and introgression with sympatric species. However, the delicate ecological balance allowing these species to co-exist may be susceptible to human-induced disruption. Conservation and recovery efforts outside of the Great Lakes should focus on maintaining minimal disturbance in and around lakes and drainage basins known to contain shortjaw cisco populations.

Some fundamental taxonomic questions remain to be addressed regarding the validity of some (and arguably all) populations of the shortjaw cisco. Until morphological or genetic markers are found that unequivocally distinguish this species from other ciscoes, skepticism about the identity of many populations will continue.

The following research and management activities are needed to clarify the status of shortjaw cisco in Alberta and throughout North America:

1) Ongoing surveys of suitable habitat are necessary to define better the range and distribution of this species. Status designations are based largely on the number of known occurrences, yet few lakes in the vast overall range of shortjaw cisco have been sampled specifically for this species. This issue is being addressed in northeastern Alberta and the data are beginning to produce a clearer picture of shortjaw cisco distribution and the size of the pool of unique genetic diversity in this portion of its range. Voucher specimens of ciscoes collected as a result of all fisheries surveys in northern Alberta should be retained and examined carefully by personnel familiar with the diagnostic characters and their variability within the species comprising this group.

2) Research directed toward resolving the taxonomic uncertainties surrounding shortjaw cisco and its allies is needed to ensure that management and recovery resources are being allocated appropriately. Effective management requires reasonable knowledge of what is being protected and an understanding of the inter-relationships between the target group and other components of the ecosystem. There is a very real possibility that some populations of what are currently recognized as the shortjaw cisco may, in fact, be forms of other species of cisco that superficially resemble the shortjaw. Only through careful morphological, genetic, and ecological evaluation of a large sample of presumed shortjaw cisco populations will this uncertainty be resolved. Again, voucher specimens of ciscoes from as many sites as possible should be collected, analyzed, and preserved in a museum for future research.

3) Localities believed to contain shortjaw cisco should be protected immediately from commercial exploitation and habitat degradation, even if conclusive taxonomic evidence supporting the identity of the population is lacking. Commercial fishing and sportfishing could have a negative impact on the shortjaw cisco population, particularly in small, northern lakes like Barrow Lake. Resource extraction activities could lead to pollution, eutrophication, excessive sedimentation, or other influences that may have a detrimental effect on cisco populations. Careful consideration should be given to the potential impacts of these activities on water bodies believed to contain the shortjaw cisco. It may be appropriate to impose a fishing closure on Barrow Lake at some time in the future.

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APPENDIX 1. Definitions of selected legal and protective designations.

A. The General Status of Alberta Wild Species 2000 (after Alberta Sustainable Resource Development 2001)

2000 Rank	1996 Rank	Definitions
At Risk	Red	Any species known to be at risk after formal assessment and designation as Endangered or Threatened in Alberta.
May Be At Risk	Blue	Any species believed to be at risk. These species will require a detailed assessment for possible formal designation as Endangered or Vulnerable.
Sensitive	Yellow	Any species known to be, or believed to be, particularly sensitive to human activities or natural events.
Secure	Green	Any species known to be, or believed to be, not at risk.
Undetermined	Status Undetermined	Any species where not enough information exists to adequately use the ranking system (exceptional cases only).
Not Assessed	n/a	Any species known or believed to be present but which have not yet been evaluated.
Exotic/Alien	n/a	Any species that have been introduced as a result of human activity.
Extirpated/Extinct	n/a	Any species no longer thought to be present in the jurisdiction or are believed to be extinct.
Accidental/Vagrant	n/a	Any species occurring infrequently and unpredictably outside their usual range.

B. Alberta's *Wildlife Act*

Species designated as "Endangered" under Alberta's *Wildlife Act* include those defined as "Endangered" or "Threatened" by *A Policy for the Management of Threatened Wildlife in Alberta* (Alberta Fish and Wildlife 1985):

Endangered	A species whose present existence in Alberta is in danger of extinction within the next decade.
Threatened	A species that is likely to become endangered if the factors causing its vulnerability are not reversed.

C. Committee on the Status of Endangered Wildlife in Canada (after COSEWIC 2002)

Extinct	A species that no longer exists.
Extirpated	A species that no longer exists in the wild in Canada, but occurs elsewhere.
Endangered	A species facing imminent extirpation or extinction.
Threatened	A species that is likely to become endangered if limiting factors are not reversed.
Special Concern	A species of special concern because of characteristics that make it particularly sensitive to human activities or natural events.
Not at Risk	A species that has been evaluated and found to be not at risk.
Data Deficient	A species for which there is insufficient scientific information to support status designation.

D. Heritage Status Ranks: Global (G), National (N), Sub-National (S) (after NatureServe 2001)

G1/N1/ S1	**Critically Imperiled**: Critically imperiled globally because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction. Typically 5 or fewer occurrences or very few remaining individuals (<1,000) or acres (<2,000) or linear miles (<10).
G2/N2/ S2	**Imperiled**: Imperiled globally because of rarity or because of some factor(s) making it very vulnerable to extinction or elimination. Typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000) or acres (2,000 to 10,000) or linear miles (10 to 50).
G3/N3/ S3	**Vulnerable**: Vulnerable globally either because very rare and local throughout its range, found only in a restricted range (even if abundant at some locations), or because of other factors making it vulnerable to extinction or elimination. Typically 21 to 100 occurrences or between 3,000 and 10,000 individuals.
G4/N4/ S4	**Apparently Secure**: Uncommon but not rare (although it may be rare in parts of its range, particularly on the periphery), and usually widespread. Apparently not vulnerable in most of its range, but possibly cause for long-term concern. Typically more than 100 occurrences and more than 10,000 individuals.
G5/N5/ S5	**Secure**: Common, widespread, and abundant (although it may be rare in parts of its range, particularly on the periphery). Not vulnerable in most of its range. Typically with considerably more than 100 occurrences and more than 10,000 individuals.
GX/NX/ SX	**Presumed Extinct** (species) - Believed to be extinct throughout its range. Not located despite intensive searches of historical sites and other appropriate habitat, and virtually no likelihood that it will be rediscovered. **Eliminated** (ecological communities) - Eliminated throughout its range, with no restoration potential due to extinction of dominant or characteristic species.
GH/NH/ SH	**Possibly Extinct** (species) - Known from only historical occurrences, but may nevertheless still be extant; further searching needed. **Presumed Eliminated** (Historic, ecological communities) - Presumed eliminated throughout its range, with no or virtually no likelihood that it will be rediscovered, but with the potential for restoration, for example, American Chestnut (Forest).

E. United States Endangered Species Act (after National Research Council 1995)

Endangered	Any species which is in danger of extinction throughout all or a significant portion of its range.
Threatened	Any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

APPENDIX 2. Glossary of terms.

Allochrony - Differences in spawning time.

Detritus - Dead or decaying organic material.

Epibenthic - Living on the surface of the substratum.

Epilimnion - The warmer, well-mixed upper layer of the water column.

Eutrophication - The process by which lakes and streams are enriched by nutrients (usually phosphorus and nitrogen) which leads to excessive plant growth– algae in the open water, periphyton (*attached* algae) along the shoreline, and macrophytes (the higher plants we often call *weeds*) in the nearshore zone. The extent to which this process has occurred is reflected in a lake's trophic classification: oligotrophic (nutrient poor), mesotrophic (moderately productive), and eutrophic (very productive and fertile). The less productive a lake is naturally, the more sensitive it is to increased nutrient loads from human-caused disturbances in the watershed.

Gillraker - Slender bony protuberances or cartilaginous projections from the gill arches that aid in the capture and ingestion of prey items. The shape and number of gillrakers can be a good indication of the fish's diet. Species that eat large prey items (such as other fishes or mollusks) often have short and widely spaced gill rakers; those that eat small prey (such as plankton) typically have long, slender, and numerous gillrakers that trap small particles more efficiently.

Hypolimnetic Zone - The bottom, and most dense layer of a stratified lake. It is typically the coldest layer in the summer and warmest in the winter. It is isolated from wind mixing and typically too dark for much plant photosynthesis to occur.

Introgression - The incorporation of genes from one species into the gene pool of another species. This requires that hybrids are viable and fertile and that backcrosses occur frequently.

Limnetic Zone - Inhabiting the open water zone.

Nuptial Tubercles - Small bumps that develop on some sexually mature fishes.

Pelagic - Inhabiting open water, typically well off the bottom. Sometimes used synonymously with limnetic to describe the open water zone (esp. in oceanic or large lake environments).

Stratified - Separated into distinct layers.

Thermocline - The depth at which the temperature gradient is steepest during the summer; usually this gradient must be at least 1°C per meter of depth.

APPENDIX 3. Shortjaw cisco localities across North America.

Specimens in museum collections

Site	Province	Lat./long.	Institution*
Great Slave Lake	Northwest Territories	61° 30' N 114° 00' W	ROM
Tazin River	Northwest Territories	60° 37' N 110° 22' W	CMN
Barrow Lake	Alberta	59° 15' N 111° 14' W	PMA, UAMZ, ROM
Reindeer Lake	Saskatchewan	57° 14' N 102° 16'W	ROM
Lake Athabasca	Saskatchewan	59° 20' N 109° 00' W	PMA, ROM
Lake Winnipeg	Manitoba	52° 08' N 97° 16' W	ROM
Big Athapapuskow Lake	Manitoba	54° 37' N 101° 39'W	ROM
Little Athapapuskow L.	Manitoba	54° 37' N 101° 39' W	ROM
George Lake	Manitoba	50° 15' N 95° 30' W	UMMZ
Churchill River	Manitoba	58° 44' N 94° 07' W	MMMN
Lake Superior	Ontario	48° 00' N 87° 00' W	ROM, UMMZ
Lake Nipigon	Ontario	49° 50' N 88° 30' W	ROM
Basswood Lake	Ontario	48° 05' N 91° 35' W	ROM
White Partridge Lake	Ontario	45° 50' N 78° 06' W	ROM
Big Trout Lake	Ontario	53° 45' N 90° 00' W	ROM
Attawapiskat Lake	Ontario	52° 18' N 87° 54' W	ROM
Loonhaunt Lake	Ontario	49° 01' N 93° 30' W	ROM
Sandy Lake	Ontario	53° 02' N 93° 00' W	ROM

Reports from the literature (unconfirmed)

Site	Province	Lat./long	Reference
Lake Athabasca	Alberta	59°15' N 110° 30' W	Dymond and Pritchard (1930)
Gregoire Lake	Alberta	56° 29' N 111° 11' W	Tripp and Tsui (1980)
Cold Lake	Alberta	54° 32' N 110° 02' W	Clarke (1973)
Flotten Lake	Saskatchewan	54° 37' N 108° 32' W	Clarke (1973)
Manistikwan Lake	Manitoba	54° 45' N 101° 46' W	Clarke (1973)
Clearwater Lake	Manitoba	54° 05' N 101° 00' W	Clarke (1973)
Lake Winnipegosis	Manitoba	52° 29' N 99° 59' W	Bajkov (1930)
Lake of the Woods	Ontario	49° 16' N 94° 40' W	Clarke (1973)
Lac Seul	Ontario	50° 20' N 92° 16' W	Clarke (1973)
Deer Lake	Ontario	52° 38' N 94° 15' W	Clarke (1973)

* ROM, Royal Ontario Museum; CMN, Canadian Museum of Nature; PMA, Provincial Museum of Alberta; UAMZ, University of Alberta Museum of Zoology; MMMN, Manitoba Museum of Man and Nature; UMMZ, University of Michigan Museum of Zoology.

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